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Research Article

Revised chronology of Trichoptera evolution*

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Abstract

Based on a recalibrated BEAST diversification time analysis, we provide a revised chronology for the evolution of major lineages of Trichoptera. Fossil evidence indicates that caddisflies evolved at least by the Norian of Late Triassic (median age 222.6 Ma), compared with our estimate of at least 201.3 Ma. The ancestors of suborders Annulipalpia and Integripalpia also evolved as early as the Norian. Fossil evidence indicates that the ancestor of subterorder Phryganides lived at least by the Aalenian of Middle Jurassic (median age 173.6 Ma), compared with our estimate of at least 174.1 Ma.

Key Words

BEAST, caddisfly, fossil, Jurassic, phylogeny, Triassic

Introduction

Speculations about caddisfly relationships, based on morphological evidence and hand calculations have been published for many years (reviewed by Morse 1997). More recently, molecular techniques have accelerated this field of enquiry (Malm et al. 2013; Kjer et al. 2016; Thomas et al. 2020; Ge et al. 2022), motivated in part by increased appreciation of the ecosystem services provided by caddisflies, especially the use of these insects in assessment of water quality (e.g. Morse et al. (2019)). An understanding of these historical relationships is useful for interpreting evolution of known functional traits of caddisflies relevant for those ecosystem services and for proposing and testing hypotheses of yet-unknown traits. In addition to re-assessing the phylogenetic relationships of caddisfly families with six independent genes and > 10 000 nucleotides, sequencing 185 species representing 49 families, Thomas et al. (2020) also estimated the ages of the resulting clades using BEAST, concluding that “the most recent common ancestor of Trichoptera appeared in the Permian (ca. 275 Ma) in line with the first appearance of Trichoptera in the fossil record and that vicariance explains the distribution of most trichopteran taxa.”

The identity and dates of many fossils were re-assessed by Nicholson et al. (2015), providing updated information for recalibrating the age estimates by Thomas et al. (2020). We report here our revised estimates resulting from those recalibrations.

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Methods

Ages of lineages were estimated by BEAST as described by Thomas et al. (2020), but recalibrated with fossil dates provided by Nicholson et al. (2015) and more recently available dates from The Paleobiology Database (2023). The phylogenetic estimate is based on the multiple sequence alignment from Thomas et al. (2020), except an unresolved node was manually constrained with findings using genomic data from Frandsen et al., in prep. Fossil families are included in the phylogeny, based on morphological evidence from Wichard and Müller (2022, for Palleptoceridae), references cited by Nicholson et al. (2015) and The Paleobiology Database (2023).

Results

Historical relationships of Trichoptera families with estimated minimum ages and fossil evidence are shown in Table 1 and Fig. 1. Thin lines indicate relationships only; their lengths are not supported by fossil evidence and are arbitrary and uninformative. Thick lines indicate the extent of fossil evidence (Nicholson et al. 2015). Solid lines show relationships according to Thomas et al. (2020) with a constraint from Frandsen et al., in prep. Broken horizontal lines show relationships based on morphological evidence only. Dots indicate re-estimates of minimum age. The re-estimated maximum age is at least 174.0 Ma for all Phryganides lineages and at least 201.3 Ma for all others.

Table 1. Revised chronology of Trichoptera from BEAST based on updated fossil records (Nicholson et al. 2015; The Paleobiology Database 2023).

	Taxa	Divergence	Family	Lower boundary	Upper (soft max)	BEAST parameters	Fossil taxa	Date and Locality Information
1	Amphiesmenoptera	Root: Lepidoptera/ Trichoptera split		>182.7	299	uniformPrior lower="182.7" upper="299.0"	*Liadotaulius maior*	From latest Lias (Earliest Jurassic) of Germany, Lias is Rhaetian to Toarcian in age (182.7–201.3 mya)
2	Lepidoptera	**Base of Lepidoptera**		>145	299	logNormalPrior mean="35.0" stdev="47.55" offset="145.0"	Appearance of Micropterigidae fossils	Boundary of Jurassic - Cretaceous, Min: uppermost Cretaceous, 145 mya; Soft max: Pterygota of Late Carboniferous, 299 mya.
3	Trichoptera	**Base of Trichoptera**		>174.1	299	logNormalPrior mean="22.98" stdev="47.2" offset="174.1"	Modern trichopteran families (Rhyacophilidae, Philopotamidae)	End of early to beginning of mid Jurassic, Min: upper mid Jurassic, 174.1 mya; Soft max: Pterygota of Late Carboniferous, 299 mya.
4	Annulipalpia (Philopotamoidea)	**Philopotamidae/ Stenopsychidae (Stem)**		**>174.1**	252.5	logNormalPrior mean="17.05" stdev="25.0" offset="174.1"	*Dolophilodes* (*Sortosella*) *shurabica*	Earliest Jurassic, from the Sai-Sagul locality (Kyrgyzstan, southern Fergana)
5	Annulipalpia (Philopotamoidea)	***Chimarra/ Chimarrhodella***	Philopotamidae	>13.82	201.3	logNormalPrior mean="50.0" stdev="52.8" offset="13.82"	*Chimarra resinae*, *C. dommeli*, *C. weitschati*, *C. palaedominicana*	Dominican amber: Burdigalian/ Langhian terrestrial amber in the Dominican Republic
6	Annulipalpia (Philopotamoidea)	***Wormaldia/Doloclanes***	Philopotamidae	>93.5	201.3	logNormalPrior mean="30.0" stdev="29.75" offset="93.5"	*Wormaldia cretacea*	Burmese amber, Early/Lower Cenomanian, Cretaceous of Myanmar.
7	Annulipalpia (Philopotamoidea)	***Philopotamus/Kisuara***	Philopotamidae	>33.9	201.3	logNormalPrior mean="40.0" stdev="50.05" offset="33.9"	*Philopotamus hamatus*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia
8	Annulipalpia (Philopotamoidea)	***Stenopsyche/ Stenopsychodes***	Stenopsychidae	**>33.9**	201.3	logNormalPrior mean="40.0" stdev="50.05" offset="33.9"	*Stenopsyche imitata*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia
9	Annulipalpia (Hydropsychoidea)	***Diplectrona/Sciadorus/* Smicrideinae**	Hydropsychidae	>33.9	201.3	logNormalPrior mean="40.0" stdev="50.05" offset="33.9"	*Diplectrona minima*, *D. ocularia*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia
10	Annulipalpia (Hydropsychoidea)	***Potamyia/Hydropsyche***	Hydropsychidae	**>46.2**	201.3	logNormalPrior mean="49.0" stdev="40.4" offset="46.2"	*Hydropsyche operta*	Chagrin Valley Green River Formation, Bridgerian (Eocene of USA), lacustrine - diatomaceous shale
11	Annulipalpia (Psychomyioidea)	***Ecnomus/Ecnomina***	Ecnomidae	**>125.45**	201.3	logNormalPrior mean="24.7" stdev="19.5" offset="125.45"	*Ecnomus cretacia*	Mdeyrij-Hammana, Casa Baabda (Azar coll), which is in a Barremian terrestrial amber in Lebanon.
12	Annulipalpia (Psychomyioidea)	***Antillopsyche/ Pseudoneuroeclipsis***	Pseudoneureclipsidae	**>93.5**	201.3	logNormalPrior mean="29.65" stdev="29.9" offset="93.5"	*Amberclipsis elegans*	Burmese amber, ZMFK coll. Early/Lower Cenomanian Cretaceous of Myanmar.
13	Annulipalpia (Psychomyioidea)	***Lype/Psychomyia/ Psychomyiella***	Psychomyiidae	**>113.0**	201.3	logNormalPrior mean="25.2" stdev="24.05" offset="113.0"	*Sententimiya wichardi*	Khasurty (Cretaceous of Russian Federation) Aptian lacustrine (Melnitsky and Ivanov 2020 in Kopylov et al. 2020)

	Taxa	Divergence	Family	Lower boundary	Upper (soft max)	BEAST parameters	Fossil taxa	Date and Locality Information
14	Annulipalpia (Psychomyioidea)	***Phylocentropus*/ *Dipseudopsis***	Dipseudopsidae	**>125.5**	201.3	logNormalPrior mean="21.1" stdev="21.1" offset="125.0"	*Phylocentropus succinolebanensis*	Lebanese amber, Hammana-Mdeyrij, Grès du Liban Formation, Late/Upper Barremian, Cretaceous
15	Annulipalpia (Psychomyioidea)	***Neureclipsis*/ *Neucentropus***	Polycentropodidae	>93.5	201.3	logNormalPrior mean="29.65" stdev="29.9" offset="93.5"	*Neureclipsis burmanica*	Burmese amber (NIGP coll), which is in a Cenomanian terrestrial amber in Myanmar. Age range: 99.7 to 94.3 Ma
16	Annulipalpia (Psychomyioidea)	***Holocentropus*/other Polycentropodidae**	Polycentropodidae	**>145.0**	201.3	logNormalPrior mean="15.6" stdev="15.55" offset="145.0"	*Polylongaevus eskovi*	Kempendyay River (Yakutiya) Khaya Formation, siltstone/ sandstone, Tithonian Jurassic of Russian Federation
17	(Spicipalpia) Ptilocolepidae	***Palaeagapetus*/ *Ptilocolepus***	Ptilocolepidae	**>89.8**	201.3	logNormalPrior mean="30.5" stdev="31.0" offset="89.8"	*Palaeagapetus furcilla*	New Jersey amber, Parlin sand pit; Turonian, Magothy Formation of NJ, USA.
18	(Spicipalpia) Hydroptilidae	***Alisotrichia*/ *Celaenotrichia***	Hydroptilidae	>13.82	201.3	logNormalPrior mean="50.0" stdev="52.8" offset="13.82"	*Alisotrichia arizela*	Dominican amber, a Burdigalian/ Langhian terrestrial amber in the Dominican Republic
19	(Spicipalpia) Hydroptilidae	***Ochrotrichia*/ *Nothotrichia***	Hydroptilidae	>33.9	201.3	logNormalPrior mean="40.0" stdev="50.05" offset="33.9"	*Ochrotrichia umbra*	Rovno Amber, Klesov locality, Priabonian, Eocene of Ukraine
20	(Spicipalpia) Hydroptilidae	***Leucotrichia*/ *Anchitrichia***	Hydroptilidae	>13.82	201.3	logNormalPrior mean="50.0" stdev="52.8" offset="13.82"	*Leucotrichia adela*	Dominican amber (USNM Brodzinsky Lopez-Pena coll) (Miocene to Miocene of Dominican Republic)
21	(Spicipalpia) Hydroptilidae	***Hydroptila*/*Oxyethira***	Hydroptilidae	>47.8	201.3	logNormalPrior mean="42.5" stdev="42.45" offset="47.8"	*Hydroptila phileos*	Cathedral Bluffs, a Bridgerian lacustrine (large shale) in the Green River Formation of Colorado.
22	(Spicipalpia) Hydroptilidae	***Agraylea* / (*Hydroptila*, *Oxyethira*)**	Hydroptilidae	**>89.8**	201.3	logNormalPrior mean="30.5" stdev="31.0" offset="89.8"	*Agraylea* (*Nanoagraylea*) *cretaria*, *A. parva*	White Oaks Pit, Turonian delta plain amber/lignite in Raritan Formation of NJ, USA
23	(Spicipalpia) Glossosomatidae	**Glossosomatidae**	Glossosomatidae	**>145.0**	201.3	logNormalPrior mean="15.6" stdev="15.55" offset="145.0"	*Dajella tenera*	
24	(Spicipalpia) Hydrobiosidae	***Atopsyche*/*Moruya***	Hydrobiosidae	>13.82	201.3	logNormalPrior mean="50.0" stdev="52.8" offset="13.82"	*Atopsyche perlucida*	Dominican amber, a Burdigalian/ Langhian terrestrial amber in the Dominican Republic
25	(Spicipalpia) Hydrobiosidae	***Isochorema*/ *Apatanodes***	Hydrobiosidae	**>33.9**	201.3	logNormalPrior mean="40.0" stdev="50.05" offset="33.9"	*Isochorema secunda*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia
26	(Spicipalpia) Rhyacophilidae	***Rhyacophila*/ *Himalopsyche* (Stem)**	Rhyacophilidae	**>83.5**	201.3	logNormalPrior mean="33.25" stdev="32.27" offset="83.5"	*Rhyacophila antiquissima*	Taimyr amber, a Santonian terrestrial amber in the Kheta Formation of Russia
27	Integripalpia (Leptoceroidea)	***Ganonema*/*Phylloicus***	Calamoceratidae	**>125.0**	174.1	logNormalPrior mean="14.2" stdev="13.3" offset="125.0"	*Anisocalamus mixtus*	Chernovskie Kopi, Doronino Formation Barremian, Cretaceous of Russian Federation, lacustrine claystone.
28	Integripalpia (Leptoceroidea)	***Molannodes*/*Molanna***	Molannidae	**>55.8**	174.1	logNormalPrior mean="33.2" stdev="32.5" offset="55.8"	*Molanna derosa*	Sunchal lacustrine - mudstone & calcareous limestone, Jujuy, Argentina, Maíz Gordo Formation, Late/Upper Paleocene
29	Integripalpia (Leptoceroidea)	***Triplectides*/ *Atriplectides***	Atriplectidae	**>33.9**	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Triplectides rudis*, *T. patens*, *T. pellucens*, *T. palaeoslavicus*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia
30	Integripalpia (Leptoceroidea)	***Marilia*/*Odontocerum***	Odontoceridae	**>33.9**	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Marilia ophthalmica*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia and Poland
31	Integripalpia (Leptoceroidea)	***Philorheithrus*/ *Psilopsyche***	Philorheithridae	**>125.0**	174.1	logNormalPrior mean="14.2" stdev="13.3" offset="125.0"	*Palaeorheithrus* sp., *Palaeorheithrus sibiricus*	Chernovskie Kopi, Doronino Formation Barremian, Cretaceous of Russian Federation, lacustrine claystone.
32	Integripalpia (Leptoceroidea)	***Plectrotarsus*/ Oeconesidae**	Plectrotarsidae	**>140.2**	174.1	logNormalPrior mean="9.3" stdev="9.4" offset="140.2"	*Palaeotarsus desertus*	Durlston Bay, Late/Upper Berriasian (Cretaceous of England), lagoonal; lithified siliciclastic sediments

	Taxa	Divergence	Family	Lower boundary	Upper (soft max)	BEAST parameters	Fossil taxa	Date and Locality Information
33	Integripalpia (Leptoceroidea)	**Leptoceridae**	Leptoceridae	**>113.0**	174.1	logNormalPrior mean="16.9" stdev="16.9" offset="113.0"	*Creterotesis coprolithica*	Zaz Formation, Baissa, Buryatia, Ruddian Federation. Ivanov 2006.
34	Integripalpia (Leptoceroidea)	***Leptocerus/ Trichosetodes***	Leptoceridae	>33.9	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Leptocerus solifemella*	Rovno Amber, a Priabonian (Eocene) terrestrial amber in Ukraine.
35	Integripalpia (Leptoceroidea)	***Ceraclea/ Brachysetodes***	Leptoceridae	>33.9	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Ceraclea* sp.	Rovno Amber, a Priabonian (Eocene) terrestrial amber in Ukraine.
36	Integripalpia (Sericostomatoidea)	***Beraeodes/(Beraea, Beraeomiya)***	Beraeidae	**>33.9**	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Beraeodes pectinatus*, *B. anglica*, *B. vectensis*	Priabonian lagoonal/shallow subtidal lime mudstone in Bouldnor Formation, UK & Baltic Amber in Russia & Ukraine
37	Integripalpia (Limnephiloidea)	***Phryganea/* Phryganeinae**	Phryganeidae	>33.9	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Phryganea dubia*, *P. egregia*, *P. fossilis*	Baltic Amber, Berendt collection, which is in a Priabonian terrestrial amber in Poland
38	Integripalpia (Limnephiloidea)	**Phryganeidae**	Phryganeidae	**>93.5**	174.1	logNormalPrior mean="25.2" stdev="21.1" offset="93.5"	*Phryganea arenifera*	Kounic, which is in a Cenomanian terrestrial shale in the Peruc-Korycany Formation of the Czech Republic
39	Integripalpia (Limnephiloidea)	**Limnephilidae**	Limnephilidae	**>113.0**	174.1	logNormalPrior mean="16.9" stdev="16.9" offset="113.0"	*Indusia reisi*	Mt. Uskuk, Ondai Sair, Anda-Khuduk Formation, Aptian (Cretaceous of Mongolia), lacustrine; shale
40	Integripalpia (Limnephiloidea)	***Limnephilus/ Hesperophylax***	Limnephilidae	>46.2	174.1	logNormalPrior mean="35.1" stdev="35.5" offset="46.2"	*Limnephilus eocenicus*, (*L. recultus*: >15.97)	Roan Mountain, Bridgerian lacustrine (large shale) in Green River Formation of Colorado, USA
41	Integripalpia (Limnephiloidea)	***Micrasema/ Brachycentrus***	Brachycentridae	**>113.0**	174.1	logNormalPrior mean="16.9" stdev="16.9" offset="113.0"	*Baissoplectrum separatum*	Baissa, an Aptian lacustrine - large marl/siltstone in the Zaza Formation of Russia.
42	Integripalpia (Limnephiloidea)	***Lepidostoma/ Theliopsyche***	Lepidostomatidae	**>125.45**	174.1	logNormalPrior mean="13.4" stdev="13.5" offset="125.45"	*Eucrunoecia ridicula*	Early/Lower Barremian, Upper Weald Clay Formation, Capel, Surrey, UK.
43	Integripalpia (Limnephiloidea)	***Goera/(Silo/Silonella)***	Goeridae	**>33.9**	174.1	logNormalPrior mean="40.0" stdev="38.2" offset="33.9"	*Goera gracilicornis*, *Silo brevicornis*	Baltic Amber, a Priabonian (Eocene) terrestrial amber in Russia

Discussion

According to Nicholson et al. (2015), amongst the family-level lineages, in Annulipalpia, the extant philopotamid lineage is represented confidently by a fossil from the Pliensbachi (J1, median age 186.3 Ma, with our estimated age greater than 174.1 Ma). Fossil families †Electralbertidae, †Protobaikalopsychidae and †Vitimotauliidae persisted during the Cretaceous. Estimated minimum ages for extant families Polycentropodidae, Dipseudopsidae, Ecnomidae, Psychomyiidae, Pseudoneureclipsidae, Hydropsychidae and Stenopsychidae were greater than 145.0, 125.5, 125.45, 113.0, 93.5, 46.2 and 33.9 Ma, respectively.

Again, according to Nicholson et al. (2015), in Integripalpia, the oldest lineage, dating from the Norian (T3, median age 222.6 Ma), is of †Necrotauliidae, a basal lineage of Integripalpia that survived to at least the Berriasian (K1, median age 142.85 Ma). Fossils of extinct families †Dysoneuridae, †Baissoferidae, †Burmapsychidae and †Cretapsychidae, †Taymyrelectronidae and †Yantarocentridae date from 173.6, 162.95, 105.8, 84.65 and 44.5 Ma, respectively. The oldest fossil of extant family Rhyacophilidae is from the Oxfordian (J3, median age 158.4 Ma., compared with our estimated age greater than 83.5 Ma). Similarly, the oldest fossils of Hydrobiosidae and Phryganeidae are from the Tithonian (J3, median age 148.15 Ma, compared with our estimated ages greater than 33.9 Ma and 93.5 Ma, respectively). Estimated minimum ages for other extant integripalpian families range from at least 145.0 Ma for Glossosomatidae to 33.9 Ma for Atriplectididae, Beraeidae, "Goeridae," Hydrobiosidae and Odontoceridae. The similar estimated age of these five integripalpian families (and annulipalpian Stenopsychidae) is curious, inviting investigations about geological and ecological conditions that may have accelerated diversification about this time.

Ge et al. (2022) provided an alternative phylogeny to that shown in Fig. 1. It was based on mitochondrial genomes and notably places Hydroptilidae at the base of the Annulipalpia clade. Confirmation of this alternative awaits further supporting evidence.

Additional information about fossil caddisflies in Burmese amber was recently provided by W. Wichard (2023).

Figure 1. Historical relationships of Trichoptera families with fossil evidence. Thin lines indicate relationships only; their lengths are not supported by fossil evidence and are arbitrary and uninformative; thick lines indicate the extent of fossil evidence (Nicholson et al. 2015; The Paleobiology Database 2023). Solid lines show relationships according to Thomas et al. (2020); broken horizontal lines show relationships based on morphological evidence only. Dots indicate re-estimates of minimum age (lower boundary). Maximum age [upper (soft maximum)] is 174.1 Ma for all Phryganides lineages, 201.3 Ma for all others. Numbers of living species, living subspecies and fossil species are from Morse (2023). Habitat(s), habit(s) and trophic relationship(s) are from Holzenthal et al. (2007) and Cummins et al. (2019). Current evidence for Integripalpia families shown within quotation marks (“Apataniidae,” “Goeridae,” “Helicophidae” and “Sericostomatidae”) indicates that they are paraphyletic.

Conclusion

To serve as a basis for interpreting functional traits of caddisflies, Fig. 1 depicts not only our current understanding of relationships of extant and fossil caddisfly families, but also general understanding of their habitats, habits and trophic relationships, based mainly on the summaries by Holzenthal et al. (2007, 2015) and Cummins et al. (2019). A manuscript interpreting the evolution of these functional traits is in preparation.

Author Contributions

Conceptualisation: JAT, PBF, JCM. Literature review: JAT, PBF, JCM. Investigation: JAT, PBF, JCM. Writing-Original draft: JCM. Writing-Review/editing: JAT, PBF, JCM.

Conflicts of Interest

The authors declare no conflicts of interest. No other persons or entities had a role in the design of the study; in the

collection, analyses or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

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